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Dietary adaptations of temperate primates: comparisons of Japanese and Barbary macaques

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Short title: Diet of temperate macaques

Abstract

Habitat, diet and leaf chemistry are compared between Japanese and Barbary macaques in order to reveal the similarities and differences in dietary adaptations of temperate primates living at the eastern and western extremes of the genus *Macaca*. Tree species diversity and proportion of fleshy-fruited species are much higher in Japan than in North Africa. Both species spend considerable annual feeding time on leaves. Japanese macaques prefer fruits and seeds over leaves and Barbary macaques prefer seeds. These characteristics are adaptive in temperate regions where fruit availability varies considerably with season, since animals can survive during the lean period by relying on leaf and other vegetative foods. The two species are different with respect to the higher consumption of herbs by Barbary macaques, and the leaves consumed contain high condensed and hydrolysable tannin for Barbary but not for Japanese macaques. Barbary macaques supplement less diverse tree foods with herbs. Because of the low species diversity and high tannin content of the dominant tree species, Barbary macaques may have developed the capacity to cope with tannin. This supports the idea that the digestion of leaves is indispensable to survive in temperate regions where fruit and seed foods are not available for a prolonged period during each year.

KEY WORDS: Barbary macaque, condensed tannin, Japanese macaque, leaf chemistry, temperate forest

Introduction

Primates originated in the tropical rain forests (Fleagle 1999), but they have radiated into various marginal habitats, such as woodlands, savanna and high mountains. Temperate forest is one of those marginal habitats harboring approximately 20 genera

within 8 families (Lemuridae, Indriidae, Cheirogaleidae, Lorisidae, Cebidae, Callitrichidae, Cercopithecidae and Hylobatidae), if we define the border between temperate and tropical regions as the tropics of Cancer and Capricorn (Fleagle 1999). Among them, five species (Japanese and Barbary macaques, Sichuan and Guizhou golden monkeys, and golden langurs) are distributed exclusively in the temperate regions (Fleagle 1999). Although temperate primates are a minority within the order, it is expected that adaptations to temperate habitat have evolved in various lineages.

Temperate forest is characterized by high seasonal variations in temperature and day length. In addition, fruiting phenology in temperate forest is more seasonal than in tropical forest (Ting et al. 2008), and the fruiting peak tends to occur in a more limited time of the year (autumn). Consequently, fruiting phenology tends to be more seasonal and predictable in temperate forest than in tropical forest (Ting et al. 2008). In the former, fruit is commonly absent for several months of the year (Herrera 1984; Hanya et al. 2004). In some tropical forests, plant reproductive phenology is aseasonal or weakly seasonal (Sakai 2002). In most tropical forests, however, fruiting peaks are predictable, but not all species peak in the same month (van Schaik et al. 1993; Ting et al. 2008). Based on a review of 51 temperate and tropical forests all over the world, fruit fall in the tropical forests is, on average, 1.71 times larger than that in temperate forests (Hanya and Aiba, in press). The proportion of fleshy-fruited species, potential foods for primates, is also smaller in temperate than in tropical forests (Willson et al. 1989). Therefore, fruit food availability (biomass of edible parts of fruits) seems to be smaller in temperate than in tropical forests.

Availability of young leaves, as well as fruits, may also be limited in temperate forests. Young leaves are usually available throughout the year in the tropics

(van Schaik et al. 1993), but the period of leaf flushing is confined to spring and early summer in temperate regions (Agetsuma 1995; Komiyama et al. 2001). Therefore, protein-rich young leaves cannot be used as a fallback food when fruits are not available, particularly in winter.

Hanya (2004) revealed that Japanese macaques have two dietary characteristics that are adaptive in temperate forests: 1) They eat substantial amounts of leaves and other vegetative parts, while fruits and seeds are only minor foods; 2) Even in the fruit-poor environments, they prefer fruits and seeds and eat them whenever they are available. To survive in a fruit-poor environment, monkeys must adapt by eating a large amount of leaf foods. In fact, the proportion of fruit-feeding time of temperate macaques (*Macaca fuscata*, *M. cyclopis*, and *M. mulatta*: 9-54%) is lower than that of tropical macaques (*M. fascicularis*, *M. radiata*, *M. nigra*, and *M. nemestrina*: 59-70%) (Hanya 2004). At the same time, preference for fruit is also useful in temperate regions because food ingested in excess of daily requirements can be saved as fat to help animals survive in the fruit-poor winter (Wada 1975). Since the fruiting phenology and climate are highly annually periodic in temperate forests, it is possible for animals to predict when to start fat deposition and how long a food shortage will last. In fact, patterns of seasonal change in deposited fat are quite similar among different populations of Japanese macaques, having peaks in early spring and late autumn, corresponding to the seasonal change in food availability (Muroyama et al. 2006). Therefore, dependence on deposited fat is a safe strategy in temperate regions, and fat deposition is in fact prevalent in temperate and arctic endotherms (Pond 1978).

This paper compares habitat, diet and leaf food selection by two species of temperate macaques, Japanese and Barbary macaques. We chose these species because

1) they are among the most-studied temperate macaques and 2) they are the most distantly located, at the eastern- and western-most extremes of the distribution of genus *Macaca*. Japanese macaques are distributed widely throughout the Japanese archipelago (30—41° N). Their habitat includes both warm-temperate broad-leaved evergreen forest and cool-temperate broad-leaved deciduous forest. They also live in coniferous forests in high mountains (Izumiyama 2002; Hanya et al. 2004). Barbary macaques live in isolated forest patches in Morocco and Algeria (31—36 ° N). They live from lowland thermophilous scrub through mid-altitude mixed deciduous and evergreen oak forest and high-altitude coniferous forest (Fa 1984b). Among the extant macaques, Barbary macaques represent a relatively ancient branch (Fa 1989). Some data on other temperate species are available, but we have not examined them in detail, as we have done for the Barbary and Japanese macaques because data for those other species are scanty, in particular habitat data.

Based on our original data and review of published articles, we examine 1) the difference in tree species diversity and composition between the two habitats; 2) the annual diet of the two species, with special reference to fruit/seed- and leaf-eating; 3) the relationship between fruit/seed availability and fruit/seed-eating in the two species, in order to clarify the preferences for fruit/seeds by these macaques; and 4) leaf chemistry of food and non-food tree leaves, in order to reveal the difference in selection criterion of leaf foods in response to the habitat differences.

Methods

Vegetation

Data on the vegetation of macaque habitats were derived from our published (Ménard

and Vallet 1988; Hanya et al. 2003) and unpublished data. Data from six sites in Japan and two sites in Algeria were compared. We sampled trees of >5 cm in diameter at breast height (DBH). The number of species and the Shannon-Wiener diversity index (Clutton-Brock 1977) were compared. In the calculation of the diversity index, each species was evaluated either by basal area or coverage. We controlled for the effect of area on species diversity by comparing plot sizes of 0.5 ha, in some cases obtained by extrapolation (Colwell and Coddington 1994), using the software program 'EstimateS'.

Diet

Annual dietary composition was compared primarily by using observational data of 12 months or more, expressing dietary composition according to feeding time. Data were available for three sites (lowland and coniferous forest of Yakushima and deciduous forest of Kinkazan) for Japanese macaques (Hill 1997; Hanya 2004; Tsuji et al. 2006) and two sites for Barbary macaques (deciduous oak forest of Akfadou and coniferous/evergreen broad-leaved forest of Djurdjura, Algeria) (Ménard 1985; Ménard and Vallet 1986). For comparative purposes, data on annual diet of three species of tropical macaques (*M. nigra*, *M. fascicularis* and *M. radiata*), studied by scan sampling (Ali 1986; Yeager 1996; O'Brien and Kinnaird 1997), are also shown. Data on monthly changes were not available for the tropical macaques. At Kinkazan, data were obtained over several years and included all 12 calendar months. At other sites, data were taken for at least 12 consecutive months. In the lowland forest of Yakushima, data were taken for 1.5 years, but we used data for only the first 12 consecutive months.

At the two North African sites, we used the scan sampling method, recording the activity of the first five animals seen every 10 min. At Yakushima, we used focal

144 sampling of adults and recorded behavior by instantaneous 1-min sampling (lowland
145 habitat) or continuous sampling (coniferous forest). At Kinkazan, both scan sampling
146 (every ten or five minutes) of all visible individuals and continuous focal-animal
147 sampling of adult females were used. There are methodological differences among the
148 studies, but for rough comparison of major food items, these can be neglected (Fragaszy
149 et al. 1992). In lowland Yakushima, annual dietary composition described by scan
150 sampling (Agetsuma and Nakagawa 1998; data not used because observations for
151 January were lacking) is similar to that obtained by focal animal sampling (Hill 1997;
152 data used in this paper). Dietary data were expressed as the proportion of the food in the
153 annual feeding time. The actual proportion of each food's intake may be different from
154 the value expressed by feeding time. However, this should not matter for comparative
155 purposes, such as the evaluations in this study. Other types of data, e.g. data
156 representing diet by energy intake or data of less than one year, were used ad libitum.
157
158 Leaf chemistry
159 Data on leaf chemistry for Japanese macaques in Yakushima are taken from Hanya et al.
160 (2007), but the data for Barbary macaques in Moyen Atlas, Morocco, are original. In
161 Yakushima and Moyen Atlas, both food and non-food leaves were sampled. In
162 Yakushima, food leaves were determined from our observational data covering a
163 one-year period in the coniferous and lowland forests (Hanya et al. 2007). For non-food
164 leaves, all of the species which appeared in two vegetation plots but were not eaten by
165 macaques were examined. The vegetation plots were 50 m × 50 m and 5 m × 1500 m in
166 lowland and coniferous forests, respectively. Both plots, although having different sizes
167 and shapes, reflect typical macaque habitat characteristics (Hanya et al. 2007). Since

there was no essential difference in leaf selection between the two habitats (Hanya et al. 2007), data on coniferous and lowland forests were combined. Leaves were sampled in September 2000, 2004 and 2005. In Moyen Atlas, leaves of all species listed in Table 6.4 of Drucker (1984) (except introduced species), representing food species and major trees in Moyen Atlas, were sampled. Among them, food leaves were determined using the comprehensive food list of Barbary macaques in Appendix II of Fa (1984a). Leaves were sampled in late September and early October 2005. The numbers of food and non-food leaf species sampled were, respectively, 24 and 54 in Yakushima and 13 and 16 in Moyen Atlas. Sampling periods were determined by the following conditions: 1) several months after the leaf flush in spring, 2) before the deciduous species shed leaves in late autumn 3) when at least some leaf eating was observed. Since the sites' sampling periods roughly matched, data were comparable.

Sampling was conducted for at least four individual trees, except when the species was rare (2 species for each area, sampled for only one tree). At least 20 leaves were sampled for each species. Collected leaves were kept in paper envelopes and brought to field stations where they were immediately dried at 40°C for 24 hours. Pre-dried leaves were kept in plastic bags and brought to the laboratory at the Primate Research Institute, Kyoto University, where they were dried again at 40°C for 48 hours by a vacuum incubator. After weighing, leaves were ground, sieved through a 0.5-mm mesh, put in plastic tubes, and kept in a desiccator.

All of the chemical analyses were done at the Primate Research Institute, Kyoto University, under the same protocol. Crude protein was determined using the Kjeldahl procedure for total nitrogen and multiplying by 6.25 (Hasegawa 1993). Crude lipid was measured as diethyl-ether extract by the Soxhlet method (Hasegawa 1993).

Crude ash was determined by ashing at 550°C (Hasegawa 1993). Neutral detergent fiber (NDF) was estimated following the methods of van Soest et al. (1991). Condensed tannin was extracted with 50% methanol and determined by the buthanol-HCl method (Porter 1989). Condensed tannin concentration was calibrated from the absorbance at 550 nm, using the known concentration of cyanidin chloride. Hydrolysable tannin extracted with 70% aqueous acetone was determined by the potassium iodine method (Willis and Allen 1998). Hydrolysable tannin concentration was calibrated as a tannic acid equivalent from the absorbance at 550 nm. The available standards of tannins substantially overestimate or underestimate tannin concentration (Rautio et al. 2007) , so the reported values of tannin are used only for comparative purposes (food vs. non-food or Yakushima vs. Moyen Atlas) in this study.

With respect to leaf chemistry, we conducted two kinds of analysis. First, in order to analyze leaf selection at each study site, we used the generalized linear model (GLM) based on whether macaques ate the species (0 = non-food, 1 = food) as a dependent variable and the above-mentioned six chemical properties as independent variables. This analysis was conducted separately for each site. All possible combinations of independent factors were examined, and the model fitness was assessed by Akaike's Information Criterion, or AIC (Burnham and Anderson 2002). We examined only the model having a ΔAIC (difference with the smallest AIC) of less than two. In order to assess the relative likelihood of these models, we calculated Akaike weight as: exp(-0.5 * ΔAIC score for that model)/sum of exp(-0.5 * ΔAIC score) for all of the models (Burnham and Anderson 2002). Second, in order to determine the difference in the chemical properties of food leaves between the two macaque species, we compared the six chemical properties of food leaves between the sites by the t-test.

Since six analyses were run, the alpha level was set to 0.05/6 = 0.0083, using Bonferroni correction (Curtin and Schulz 1998).

Results

Habitat

Habitats of Japanese macaques were richer in tree species, in particular fleshy-fruited species, than those of Barbary macaques, although the same genera or families were often dominant in both regions. When comparing the number of species per 0.5 ha, the Japanese forests had 18-61 tree species, including 7-35 fleshy-fruited species. On the other hand, the North African forests had only four or five tree species (all non-fleshy). As for the diversity index, quantitative comparison is difficult due to the difference in plot size and sampling method (basal area is used in most of the Japanese forests, and coverage is used in the North African forests). However, all of the Barbary macaque habitats had lower diversity indices than the Japanese macaque habitats (Table I). In one study site where the diversity index was calculated from both coverage and basal area, coverage resulted in a higher index than did basal area. If this held true for North African sites, the difference in diversity between Algeria and Japan may have been larger than shown in Table I. Even when a much broader area was covered (84 forests over 20 km×70 km), both number of species and diversity were lower in the Barbary macaque habitat (Ajbilou et al. 2006) than in any of the Japanese macaque habitats. Fleshy-fruited species constituted more than half of the tree species in Japanese forests but only a small portion (0-33%) in North African forests. In both habitats, oaks (*Quercus*) were dominant in lowlands and conifers (*Cedrus* and *Pinus* in North Africa and *Abies*, *Cryptomeria* and *Tsuga* in Japan) were dominant in high-altitude forests.

240

241 Diet

242 Among the five populations, the proportion of time spent feeding on leaves was highest
243 for Barbary macaques in the coniferous/evergreen broad-leaved forest of Djurdjura
244 (48%) and second highest in Japanese macaques in the coniferous forest of Yakushima
245 (41%) (Fig. 1). The proportion of time spent feeding on seeds was highest for Japanese
246 macaques in the deciduous forest of Kinkazan (44%), followed by two Barbary
247 macaque populations (26% and 32%) and Japanese macaques in the lowland forest of
248 Yakushima (34%); however, this value was low in the coniferous forest of Yakushima
249 (4%). The proportion of fruit-eating time was higher for Japanese macaques (10-24%)
250 than Barbary macaques (0.8-4.3%). Lichen constituted a considerable proportion of
251 feeding time of the Barbary macaques in the deciduous oak forest of Akfadou (14%). It
252 has not been reported that Japanese macaques eat lichens. In the coniferous forest of
253 Yakushima, the macaques also spend considerable time feeding on mushrooms (14%).
254 Compared with tropical macaques, time spent feeding on fruits was considerably lower
255 (54-67% for tropical vs. 0.8-25% for temperate macaques).

256 Barbary macaques eat more herbs than Japanese macaques. Barbary macaques
257 in the coniferous/evergreen broad-leaved forest of Djurdjura spent 54% of their annual
258 feeding time on herbs, constituting 35% leaves, 8% root and 11% seeds, and those in the
259 deciduous oak forest of Akfadou spent 32% of feeding time on herbs (19% leaves, 7%
260 roots and 6% seeds) (Ménard 2002). Japanese macaques in the coniferous forest of
261 Yakushima spent only 15% of annual feeding time on herbs (9% leaves, 3% roots, 1%
262 seeds) (Hanya 2004), and those at Kinkazan spent 28% of annual feeding time on herbs
263 (leaves 25% and fruits 3%) (Tsuji et al 2006; Tsuji et al. unpublished data). Hill (1997)

264 does not report the herb feeding time. However, according to Agetsuma and Nakagawa
265 (1998), who reported the food composition of Japanese macaques in the lowland of
266 Yakushima for 11 calendar months, herb feeding time was only 3% of the annual
267 feeding time.

268 Seasonal changes in diet were similar in the two species, although the
269 absolute feeding time was considerably different (Fig. 2). In the case of Japanese
270 macaques, leaf eating was dominant in winter (January-March) or spring (April-June),
271 since fruits and seeds were not available and macaques ate mature leaves as fallback
272 foods (Hanya 2004) or because protein-rich young leaves are available. Fruit and seed
273 eating occurred most often in autumn (September-November) and intermediately in
274 summer (July and August, except in the coniferous forest of Yakushima).
275 Mushroom-eating was observed in various months for Japanese macaques, most often
276 in summer. In summary, Japanese macaques ate young leaves in spring, various foods
277 such as fruits, mature leaves, fungi, seeds and animals (mostly insects) in summer, and
278 fleshy fruits and seeds (in particular acorns) in autumn. In winter, after consuming the
279 fruits and seeds produced in the preceding autumn, they ate mature leaves of evergreen
280 trees in evergreen forests or bark and winter buds in deciduous forests. The same pattern
281 has also been reported at other sites, such as the warm-temperate forest of Koshima or
282 the cool-temperate forest of Shiga Heights (Suzuki 1965; Iwamoto 1982). Barbary
283 macaques also ate leaves in spring, various foods such as fruits, seeds, leaves, lichens
284 and roots in summer, acorns and conifer (*Abies* and *Cedrus*) seeds in autumn, and leaves
285 and lichens (Akfadou only) in winter. Similar patterns have been reported from Rif or
286 Moyen Atlas (Drucker 1984; Mehlman 1988; Ménard and Qarro 1999).

287 Japanese macaques prefer fruits and seeds, while Barbary macaques also

prefer seeds but not fruits. It has already been shown that Japanese macaques in the coniferous forest of Yakushima increased their feeding time on fruits and seeds with increasing availability (Hanya 2004). We analyzed the relationship between fruit/seed eating and availability for Barbary macaques in Moyen Atlas using the data by Drucker (1984), expressing monthly dietary composition by energy intake. They ate fleshy fruits of lianas from February to April and acorns from August to November. Monthly feeding time on seeds and seed availability correlated significantly ($r = 0.969$, $P < 0.0001$). However, correlation between the monthly feeding time on fruits and fruit availability was not significant ($r = 0.569$, $P = 0.523$).

Leaf chemistry

Condensed tannin and lipid content affected leaf selection of Japanese macaques, but no chemical factor significantly affected leaf selection of Barbary macaques (Tables II and III). GLM analysis revealed that all of the models having Δ AIC < 2 included condensed tannin, hydrolysable tannin, and crude lipid (all negative effect), and thus the effects of these three factors were robust. On the other hand, in the analysis of Barbary macaques, a null model having no independent factor had the smallest AIC, and none of the other models having Δ AIC < 2 were significant.

In comparing food leaves between Japanese and Barbary macaques (Fig. 3), the food leaves of Barbary macaques included significantly higher condensed tannins, hydrolysable tannin, and crude lipid (condensed tannin: $t = 3.92$, $P = 0.004$; hydrolysable tannin: $t = 3.13$, $P = 0.0035$; crude lipid: $t = 4.17$, $P = 0.0002$). On the other hand, the content of crude protein, neutral detergent fiber and crude ash did not differ significantly between the two macaques (crude protein: $t = 2.12$, $P = 0.041$;

312 neutral detergent fiber: t = 2.75, P = 0.0093; crude ash: t = 0.838, P = 0.41).

313

314 Discussion

315 We established that tree species diversity, in particular fleshy-fruited species, is higher
316 in Japan than in North Africa. Both Japanese and North African forests are dominated
317 by *Quercus* (lowland) and conifers (high altitude forests), but North African forests
318 consist almost exclusively of those dominant species. This difference significantly
319 affected the feeding ecology of the two macaque species.

320

321 Similarities

322 In response to the pronounced seasonal changes in temperature and fruiting phenology,
323 which is a more-or-less universal pattern among temperate forests (Ting et al. 2008),
324 both Japanese and Barbary macaques showed qualitatively similar patterns of seasonal
325 dietary change. They eat young leaves in spring, various foods including fruits, mature
326 leaves, and fungi in summer, fruits and/or seeds in autumn, and leaves and other
327 vegetative foods such as mature leaves, buds and bark in winter. A similar pattern can
328 also be seen for Taiwanese macaques (Su and Lee 2001). The dietary pattern of rhesus
329 macaques in Pakistan seems a bit different; since they increase fruit eating in the
330 monsoon season (July-September) between dry early summer and dry autumn
331 (Goldstein and Richard 1989). In this area, the greatest fruit diversity and biomass is
332 available for macaques in the monsoon season (Goldstein and Richard 1989).

333 Barbary macaques share many dietary characteristics with Japanese macaques,
334 which have been proposed by Hanya (2004) as adaptive strategies to survive in
335 temperate habitat. Barbary macaques also rely considerably on leaves. It is known that

336 primates in Asia, in particular cercopithecines, tend to use leaves as fallback foods
337 compared to primates in other regions (Hemingway and Bynum 2005). The dependence
338 on leaves may have been an important prerequisite for macaques to survive in temperate
339 forests. At the same time, they prefer seeds, which contain less fiber and more digestible
340 carbohydrates than leaves (Janson and Chapman 1999), such as those of *Quercus*,
341 *Cedrus* and fir (*Abies*), and they eat them whenever available. Although this tendency
342 was statistically confirmed for only Moyen Atlas, Ménard (2002) mentioned that in
343 North African forests, acorns are available from autumn to winter, which coincides with
344 the acorn-eating period of Barbary macaques. Likewise, fir seeds are a major
345 component of the Barbary macaque diet in the Rif Mountains when they are abundant
346 (Mehlman 1988).
347
348 Differences
349 Japanese and Barbary macaques differ with respect to their degree of reliance on herbs
350 and fleshy fruits, and their leaf selection. These differences seem to be related to the
351 lower tree species diversity in North Africa than in Japan.
352 Barbary macaques rely on herbs more than do Japanese macaques. Barbary
353 macaques compensate for low tree species diversity by consuming herbs. In the two
354 North African forests (Djurdjura and Akfadou), the two most dominant species
355 (*Quercus* and *Cedrus*) account for more than 95% of the trees in coverage (Ménard and
356 Vallet 1988). Barbary macaques eat the leaves and seeds of both species, but seeds are
357 available only for a limited period. Leaves of herbs may be more palatable than tree
358 leaves due to their low fiber (Waterman 1984). In addition, excessive consumption of
359 the leaves of one or a few species may overload the detoxifying capacity of animals for

a particular toxin contained in the leaves (Janson and Chapman 1999). Japanese macaques at Kinkazan relied more heavily on herbs than those at Yakushima. The forests of Kinkazan have been degraded by overgrazing of sika deer, and some forests were converted to grasslands (Tsuji and Takatsuki 2004), so Japanese macaques also supplement their diet with herbs when food resources are scarce. Even stronger dependence on herbs has been reported for another temperate primate, the rhesus macaques in northwest Pakistan (Goldstein and Richard 1989). They live in a degraded habitat where vegetation has been damaged by logging, overgrazing by cattle, and natural disturbances. Feeding on herbs constituted 68% of the total feeding time of this population. Macaques mostly utilize forest habitat (Hanya et al. 2002), but they seem to be able to subsist largely on herbs, especially in poor temperate habitats.

Both Barbary and Japanese macaques often consumed considerable amounts of seeds, but most populations consumed fruits when they were available (Fig. 2). Seeds preferred by Barbary macaques came from the dominant plants of the forest (e.g. *Quercus*, *Cedrus* and *Abies*), whereas fleshy-fruited species were only a minority of the community. Therefore it was difficult to determine whether Barbary macaques actually preferred fleshy fruits over seeds. On the other hand, Japanese forests harbor many fleshy-fruited tree species. Many of these are common and supply a considerable amount of food for the macaques (Hanya et al. 2003).

Chemical properties, as well as relative availability, affect the selection of food leaves by Japanese macaques (Hanya et al. 2007). In North Africa, however, the effect of chemical properties may be masked by the effect of uncertain availability. The more palatable leaves may be simply not available for the Barbary macaques in this low-diversity forest.

We found that Japanese macaques avoided leaves with high condensed tannin, hydrolysable tannin, and crude lipid content. It is not evident why Japanese macaques avoided leaves with high crude lipid, but they may dislike the non-fat constituents included in crude lipid, such as waxes, cutins and pigments (Bleisch et al. 1998). On the other hand, the food leaves of Barbary macaques contained more tannin (both condensed and hydrolysable) and crude lipid than those eaten by Japanese macaques. In Yakushima, coniferous leaves, such as *Abies*, *Tsuga* and *Cryptomeria*, contain large amounts of condensed tannin (1.9%, 1.3% and 0.5%, respectively), and Japanese macaques never eat these leaves. The condensed tannin contents of these leaves were 4.1-15.7 times higher than the average for the food leaves (0.12%). In Moyen Atlas, conifer leaves such as *Cedrus* and *Juniperus* also contain much condensed tannin (2.4% and 3.7%, respectively), but Barbary macaques eat conifer leaves not only in Moyen Atlas but also in other habitats, such as Rif (Mehlman 1988) and Djurdjura (Ménard and Vallet 1986). In addition, condensed tannin content was higher in Moyen Atlas than in Yakushima not only for dominant species but also on average. The same pattern was found for hydrolysable tannins (Hanya et al., unpublished data). Barbary macaques survive in an environment where tree species diversity is low and leaves contain much tannin. On the other hand , most Japanese macaque habitats are covered with broad-leaved trees, and conifers are dominant only in high mountains (Yamagiwa and Hill 1998). However, broad-leaved trees are available even in coniferous forest (Table I), so Japanese macaques do not need the capacity to tolerate high levels of condensed tannin. It remains an open question whether Barbary and Japanese macaques have developed different detoxifying abilities for tannins. Interestingly, similar situations are reported in two species of closely related rodents (Skopec et al. 2008). However, the

408 evidence is equivocal, since specialists on tannin-rich oaks are known to have higher
409 detoxifying abilities for tannins than sympatric generalist species, but these two species
410 showed similar responses of body weight and survival in a feeding experiment on oak
411 leaves (Skopec et al. 2008). Experimental studies are necessary for the two macaque
412 species.
413
414 Conclusions and future directions in the study of temperate primates
415 This study has shown that both Japanese and Barbary macaques adapt to
416 temperate habitats in similar ways. They spend much time eating leaves and other
417 vegetative foods and select seeds and fruits when they are available. Barbary macaques
418 appear to have a high tolerance for secondary compounds in leaves, which may be
419 expected in their environment with lower tree species diversity. Animals can survive
420 during the lean period by consuming leaf and other vegetative foods and by
421 metabolizing the fat deposited from eating fruits and seeds during the food-abundant
422 period. This will lead to decreases in body weight during winter (Wada 1975; Kurita et
423 al. 2002). Such dietary switching is a common response to the deterioration of food
424 resources in many tropical forests as well (van Schaik and Pfannes 2005). It has already
425 been reported that the degree of seasonal dietary variability increases with increasing
426 latitude (Hemingway and Bynum 2005), and our close examination of the two
427 temperate species confirmed this. Temperate primates may show the extreme of this
428 strategy because of the prolonged period of fruit scarcity and the lack of fallback fruits,
429 such as *Ficus* or *Musanga*, which are often available to tropical primates even when
430 other fruits are not available (Terborgh 1983; Furuichi et al. 2001). In fact, Japanese and
431 Barbary macaques depend on leaf and other vegetative foods (45% and 55% of diet,

respectively, for one population of each), as do the "folivorous" colobines (average for 24 species: 52% of diet) (Kirkpatrick 1999). These temperate macaques consume no fruits/seeds and rely exclusively on fallback foods such as fibrous foods and lichen in some months of the year (Fig. 2), a pattern not seen in tropical macaques (Ali 1986; Yeager 1996; O'Brien and Kinnaird 1997). Therefore, leaves and lichen are 'staple', not 'filler' fallback foods for temperate macaques (Marshall and Wrangham 2007). Fat deposition is commonly reported for temperate endotherms (Pond 1978), including Japanese macaques (Wada 1975), but data on this are scarce for tropical primates. Interestingly, fat deposition has been reported in orangutans living in a habitat experiencing considerable supra-annual mast fruiting (Knott 1998). Future work on physiological and genetic analyses of fat deposition, digestion and detoxification abilities of temperate macaques would further support our conclusion.

In order to generalize these findings, more work is needed on other species. A comparison with *Rhinopithecus*, another lineage radiated in temperate regions, would be particularly interesting. The dependence on leaves and the preference for fruits are compatible in macaques because they are caeco-colic-fermenters which can digest both leaves and fruits (Lambert 1998), but this may not be so in the case of forestomach-fermenting colobines. Interestingly, *Rhinopithecus* prefer young leaves but rely heavily on lichens as fallback foods (Grueter et al. 2009), which are also eaten by Barbary macaques. Lichens are composed of largely water-soluble carbohydrates, whose digestibility is higher than NDF (Kirkpatrick et al. 2001), so they might be a better food than mature leaves. A comparison between *Macaca* and *Rhinopithecus* would be useful in helping us understand the kinds of adaptations required for primates to survive in temperate forests.

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631 Kalimantan Tengah, Indonesia. Int J Primatol 17: 51—62.
632

Table I. Number of tree species and diversity in Japanese and north African forests

Study site	Country*	Vegetation	Area (ha)	#Tree Species	#Fleshy-fruited tree species	#Tree Species/0.5 ha**	#Fleshy-fruited tree species/ 0.5ha**	H (BA based)	H (cover based)	Dominant species (Top3)	Source
Yakushima, 100 m	J	Evergreen broad-leaved forest	0.5	52	31	52	31	3.17	-	*Ardisia sieboldii* (Myrsinaceae), *Lithocarpus edulis* (Fagaceae), *Litsea acuminata* (Lauraceae)	Takafumi, Agetsuma, Tsujino, unpublis
Yakushima, 600 m	J	Evergreen broad-leaved forest	0.25	18	10	18	10	2.04	-	*Distylium racemosum* (Hamamelidaceae), *Quercus salicina* (Fagaceae), *Neolitsea aciculata* (Lauraceae)	Hanya *et al*. (2003)
Yakushima, 1050 m	J	Coniferous/evergreen broad-leaved forest	0.5	21	10	21	10	2.10	2.57	*Abies firma* (Pinaceae), *Cryptomeria japonica* (Taxodiaceae), *Tsuga sieboldii* (Pinaceae)	Hanya, unpublished
Koshima	J	Evergreen broad-leaved forest	0.5	55	35	55	35	2.45	-	*Machilus thunbergii* (Lauraceae), *Podocarpus macrophyllus* (Podocarpaceae), *Prunus jamasakura* (Rosaceae)	Go, unpublished
Shiga Heights	J	Deciduous broad-leaved forest	0.22	48	10	61	13	2.97	-	*Betula ermanii* (Betulaceae), *Quercus crispula* (Fagaceae), *Fagus crenata* (Fagaceae),	Wada, unpulished
Muroo	J	Deciduous broad-leaved forest	0.04	14	5	25	7	2.25	-	*Quercus serrata* (Fagaceae), *Quercus glauca* (Fagaceae), *Acanthopanax sciadophylloides* (Araliaceae)	Yamada, unpublished
Akfadou	A	Deciduous oak forest	0.5	4	0	4	0	-	0.77	*Quercus afares* (Fagaceae), *Quercus faginea* (Fagaceae), *Quercus suber* (Fagaceae)	Ménard and Vallet (1988)
Djurdjura	A	Coniferous/evergreen broad-leaved forest	0.5	5	0	5	0	-	0.73	*Cedrus atlantica* (Pinaceae), *Quercus ilex* (Fagaceae), *Pinus clusiana* (Pinaceae)	Ménard and Vallet (1988)
Northen Morocco (Rif)	M	Mixed oak evergreen and semidiciduous forests	NA***	15	5	-	-	1.85	-	*Pinus pinaster* (Pinaceae), *Quercus canariensis* (Fagaceae), *Quercus coccifera* (Fagaceae)	Ajbilou *et al*. (2006)

H: Shannon-Wiener's diversity index, calculated by the proportion of of each species either as basal area (BA) or coverage.
*: J: Japan, A: Algeria, M: Morocco
**: Underlined are estimated values by the method of Colwell and Coddington (1994)
633 ***: Vegetation data of 84 forests of northern Morocco (scattered over an area of 20 km*70 km), sapmled by 'nearest neighb

634

Table II. Summary of the generalized linear models on the effect of chemical properties on leaf food selection

a) Japanese macaques in Yakushima

Adopted factors	AIC	△AIC	Akaike weight
Protein+, Lipid-, Condensed-, Hydrolysable-	**75.4**	**0.0**	**21%**
Ash+, Lipid-, Condensed-, Hydrolysable-	**76.9**	**1.6**	**9%**
Lipid-, Condensed-, Hydrolysable-	**77.0**	**1.7**	**9%**
Protein+, Lipid-, Condensed-, Hydrolysable-	**77.1**	**1.7**	**9%**
Protein+, NDF+, Lipid-, Condensed-, Hydrolysable-	**77.4**	**2.0**	**8%**

b) Barbary macaques in Moyen Atlas

Adopted factors	AIC	△AIC	Akaike weight
(Null model)	43.1	0.0	8%
Condensed+	44.2	1.2	5%
Hydrolysable-	44.3	1.2	4%
Protein-	44.4	1.4	4%
Ash+	44.6	1.5	4%
Ash+, Condensed+	44.7	1.7	4%
Lipid-	45.0	1.9	3%
NDF-	45.0	2.0	3%

Protein: crude protein; NDF: neutral detergent fiber; Ash: crude ash; Lipid: crude lipid; condensed: condensed tannin; Hydrolysable: hydrolysable tannin
△AIC: Difference with the smallest AIC
Akaike weight: $\exp(-0.5*\triangle AIC)/\Sigma \exp(0.5*\triangle AIC)$ (Burnham and Anderson, 2002)
+ denotes positive effect (more likely to select as a food) and - denotes negative effect on food selection.
635 Bold indicates that the model is significant (compared with the null model).

636

Table III. Best-fit generalized linear model on the effect of chemical properties on leaf food selection

a) Japanese macaques in Yakushima

Adopted factors	Coefficient	SE	p
Crude protein	19.4	10.5	0.064
Crude lipid	-37.8	14.2	0.01
Condensed tannin	-387	139	0.0053
Hydrolysable tannin	-24.5	12.4	0.048

In this best-fit model, df=72, AIC=75.4, $p<0.0001$ in the likelihood ratio test using χ^2 distribution
Coefficient: coefficient by maximum likelihood estimation; SE: standard error of the coefficient, p: the probability that the coefficient is not different from zero by Wald test.

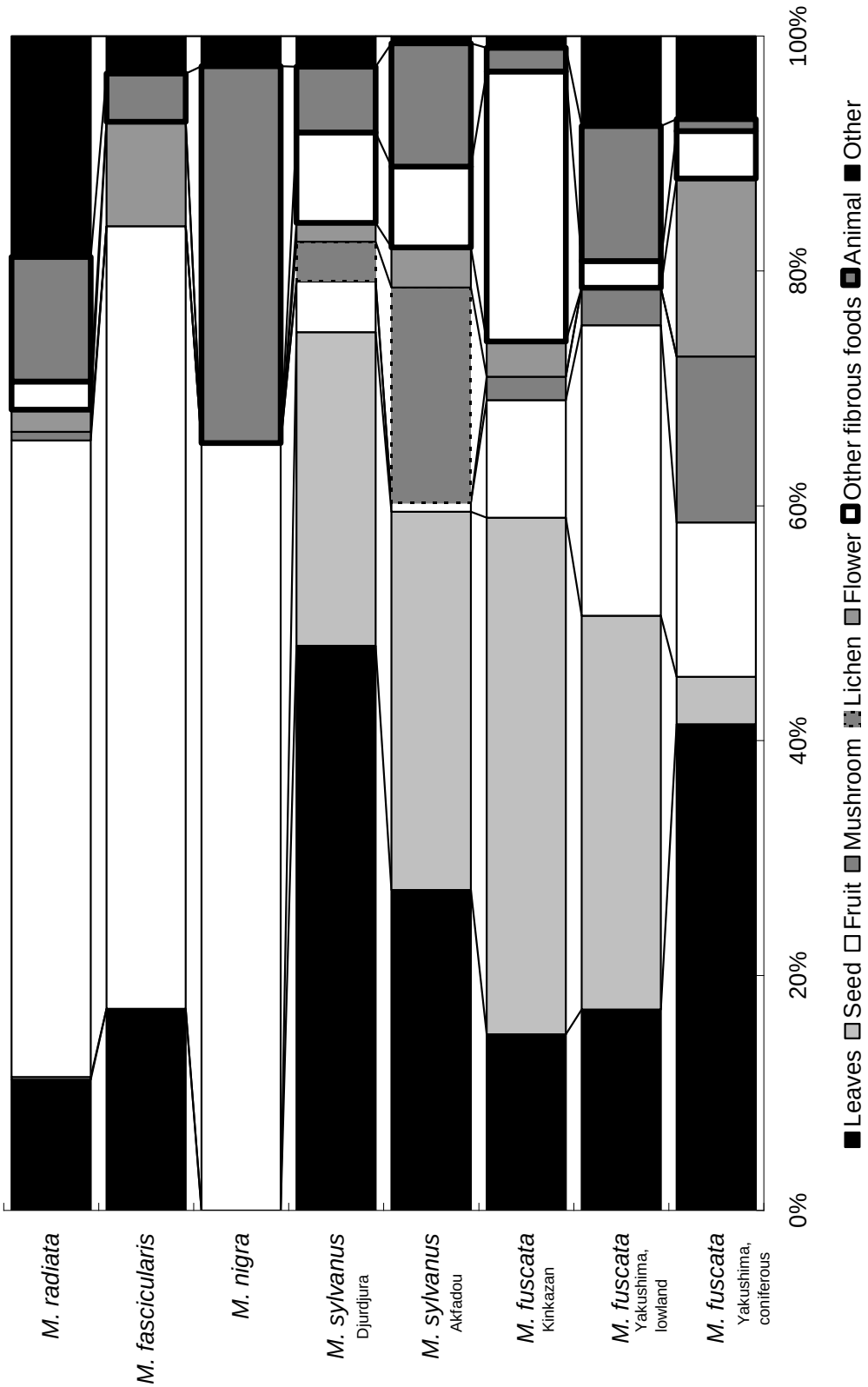
b) Barbary macaques in Moyen Atlas
637 Null model had the smallest AIC: AIC=43.1

638 Legends for figures

639 Fig. 1. Comparisons of annual diet of temperate and tropical macaques. Percentage to
640 total annual feeding time of each food category is shown. Data from (Ménard
641 1985; Ali 1986; Ménard and Vallet 1986; Yeager 1996; Hill 1997; O'Brien and
642 Kinnaird 1997; Hanya 2004; Tsuji et al. 2006).

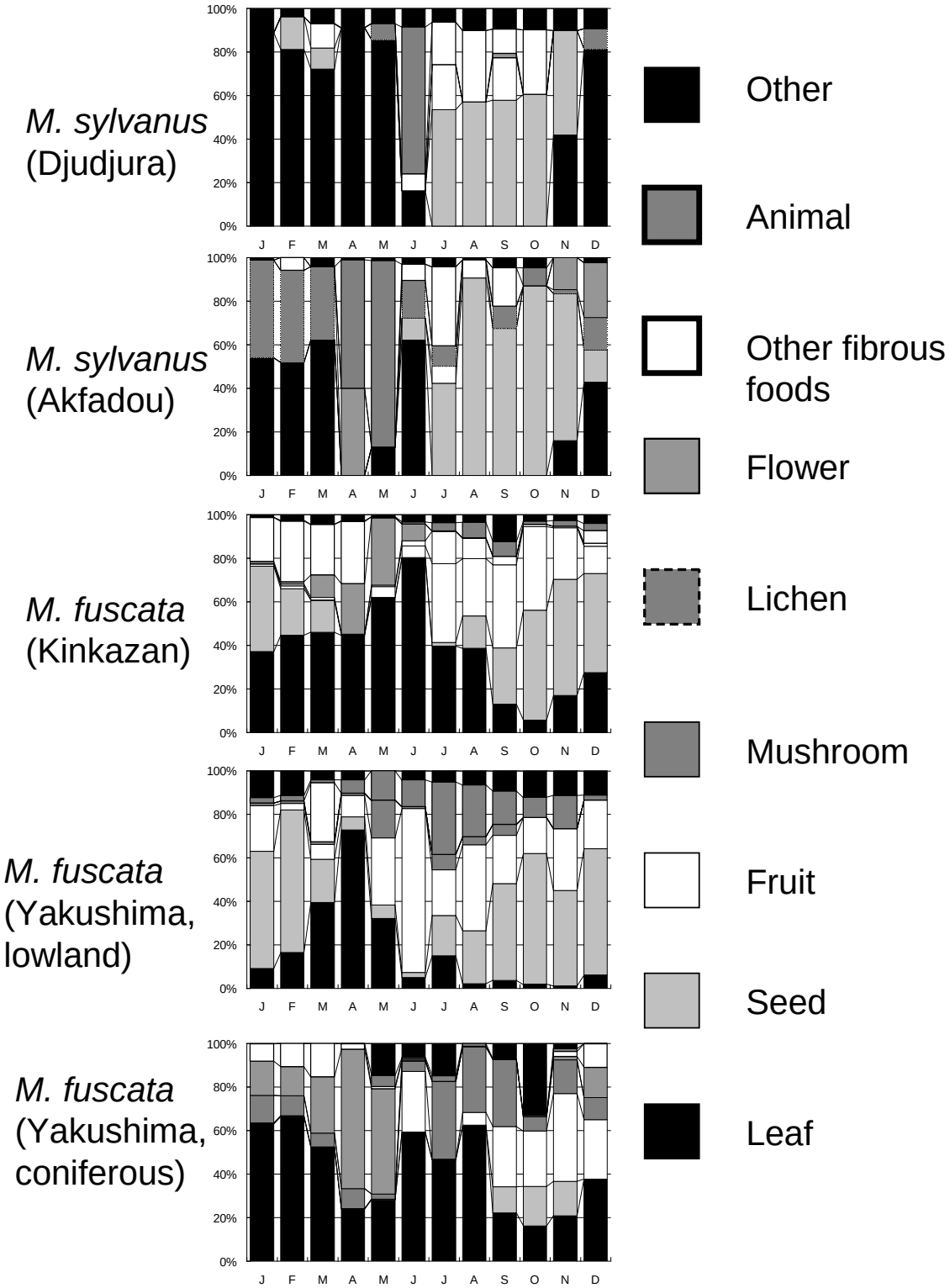
643 Fig. 2. Seasonal variations in the diet of Japanese and Barbary macaques. Percentage to
644 total monthly feeding time of each food category is shown. Data from (Ménard
645 1985; Ménard and Vallet 1986; Hill 1997; Hanya 2004; Tsuji et al. 2006).

646 Fig. 3. Leaf chemistry of food and non-food leaves of Yakushima (Japanese macaques)
647 and Moyen Atlas (Barbary macaques). Y-axis is the proportion of dry matter.
648 Average+SD is shown. Note that the scale is different among graphs.



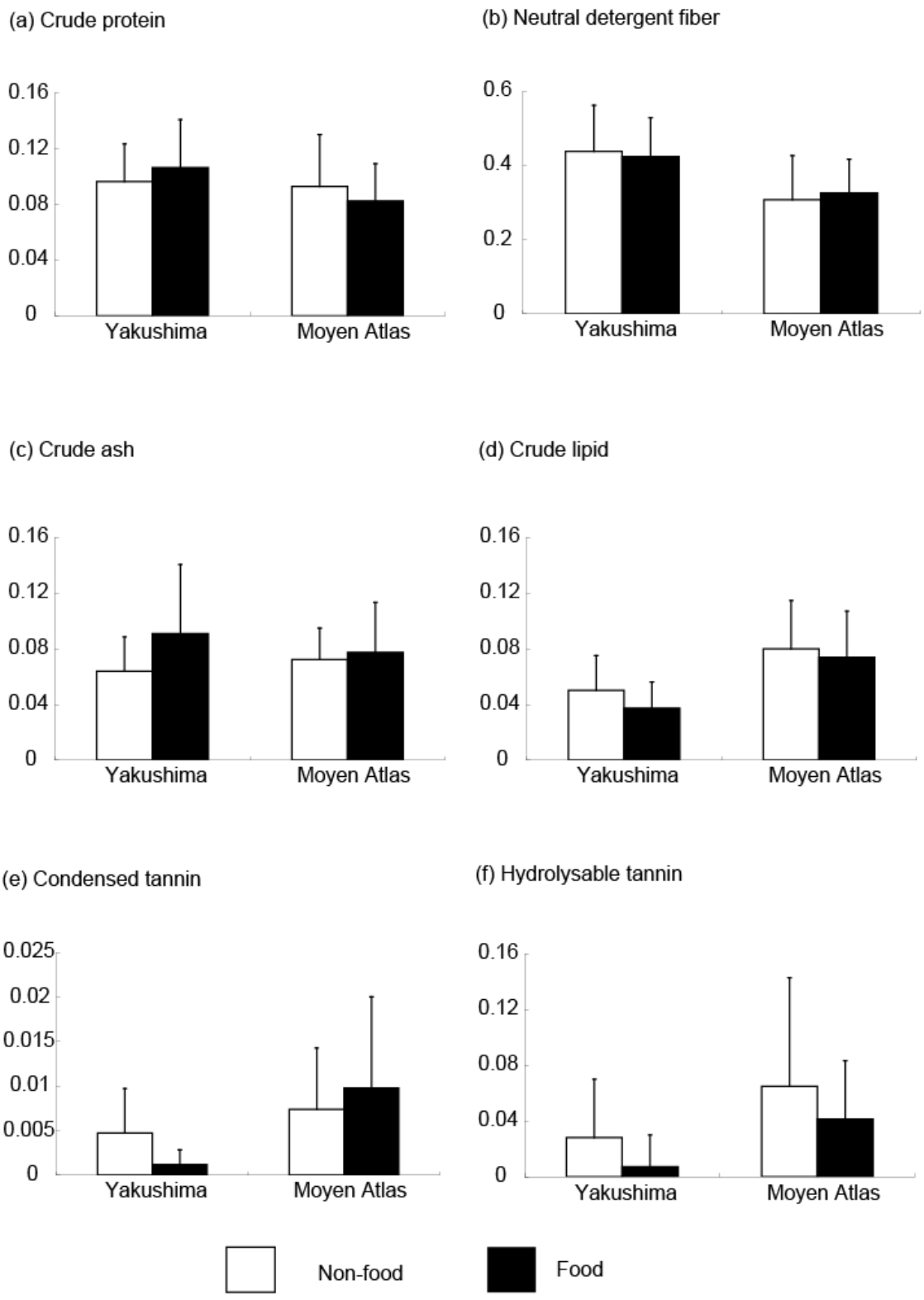
649

650 Fig. 1



651

652 Fig. 2



653

654 Fig. 3